The Functional Habitat Concept does apply to fish assemblages of the regulated Lower Ord River, Western Australia

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This paper tests the applicability of the Functional Habitat Concept (FHC) to the fish fauna of the regulated Lower Ord River (LOR), a highly regulated lowland tropical river in the remote Northern Province of the Kimberley region of Western Australia. The underlying tenet of the FHC is that in-stream hydrological and physical processes form distinct habitats, and where these habitats support distinct faunal assemblages they are considered 'functional' habitats. Eight 'potential' in-stream habitats were identified in the LOR on the basis of their physical properties across wet and dry seasons. Multivariate and species preference analysis of fish data indicated deep and shallow water habitats supported distinct fish assemblages. Shallow water habitats were characterised by small-bodied species and juveniles of large bodied species, while deep water habitats supported adults of smaller species and large-bodied fishes. Four 'functional' habitats were identified in the dry season (shallow backwaters, gravel-cobble runs, flooded riparian vegetation and channel pools). Most (except channel pools) were also discernable in the wet season, together with emergent macrophyte habitat. Individual species and life stages demonstrated clear habitat preferences, with shallow water habitats supporting greater species richness than deep water habitats. Between habitat differences were greatest in the dry season, as was the number of species with significant preferences to specific habitats. Given the importance of shallow water habitats, and their susceptibility to impacts from further abstraction, environmental flows for the LOR must be designed to protect and maintain the current distribution and area of these key habitat types to maintain their dependent faunas. In a region where the fauna has been little studied, the FHC potentially aids in the preservation of fish diversity as it identifies critical functional habitats for managers to maintain.

KEYWORDS: Kimberley, environmental flows, river management, tropical river

INTRODUCTION

Rivers in the remote north of Australia are relatively free from the pressures of development affecting those in the south of the continent (*i.e.* impoundment, regulation, abstraction and diversion) (WRC 1997). However, Australia is experiencing a drying climate (Kirono *et al.* 2011), and there is mounting pressure to develop these rivers, particularly for irrigated agriculture (Storey & Trayler 2006). The tyranny of distance from major population centres also means that these northern Australian systems have been seldom studied, with relatively little known of their ecologies compared with their counterparts in more southern climes. As a result, river managers have a poor knowledge base on which to make decisions, such as determining environmental flows (Trayler *et al.* 2002; Storey & Trayler 2006; Arthington *et al.* 2006). Gathering the necessary ecological information can be a time consuming exercise, and in the face of pressing development, an alternative approach is required. Working at the habitat level may be such an approach.

The process of dividing streams into habitat types is widely used in restoration ecology, biological monitoring and fishery management, and this practice is based on the acceptance of the assumption that habitats have some consistent ecological meaning, and working at the habitat level will "make [the system] easier to study, understand

or manage" (Rabeni *et al.* 2002). The acceptance of the linkage between species richness and habitat diversity is well entrenched in theoretical ecology (see Rabeni *et al.* 2002 and references therein), to the point where habitat is used as a surrogate for diversity; with management of habitats being the pragmatic goal. Therefore, habitats are proving useful for river survey, management and rehabilitation, as they provide a rapid and effective source of information of sufficient detail to assess the ecosystem without the need for painstaking identification of fauna or complex hydraulic modelling (Kemp *et al.* 2000).

As noted by Kemp *et al.* (2000), biological communities of rivers have been well studied over many years by ecologists, as have the processes and dynamics of channel morphology and hydraulics by hydrologists and geomorphologists. But, it is only in recent years that these parallel fields in stream ecology and geomorphology have been linked, especially in relation to habitats (Buffagni *et al.* 2000; Sullivan *et al.* 2004; Vezza *et al.* 2012).

The importance of habitats in fish ecology is well documented and has influenced the development of approaches for rapid bioassessment of river health using fish (Kennard *et al.* 2006; Parasiewicz 2007a, b). Very strong relationships have been reported between fish and habitat diversity (Joy & Death 2003; Pratt & Smokorowski 2003; Kennard *et al.* 2006; Rayner *et al.* 2008; Troia & Gido 2013). Water depth, velocity, substrate composition and cover have all been reported as key variables influencing

fish diversity, with decreases in diversity occurring in association with reduced habitat diversity (Jowett & Richardson 1995; Smith & Kraft 2005; Stefferud *et al.* 2011). Essentially, different species of fish occupy different spatial units, with separation occurring vertically based on morphology, ontogeny and feeding habit (Moyle & Vondracek 1985; Gozlan *et al.* 1998; Jackson *et al.* 2001). In regulated rivers, habitat relationships have historically been used in the determination of environmental flows by calculating 'habitat suitability curves' for individual species (Capra *et al.* 1995; Jowett & Richardson 1995; Stewart *et al.* 2005). This approach has been useful for managing systems for single species, but requires detailed autecological information and is therefore prohibitive for systems supporting high species diversity.

One of the products of the collaboration between ecologists and hydrologists has been the Functional Habitat Concept (FHC), which grew out of the known association between the quality of in-stream habitats and the diversity of species they support (Harper & Everard 1998; Newson & Newson 2000). The concept was principally developed for managing macroinvertebrate assemblages, and is based on the assumption that conserving habitats ultimately conserves biodiversity (Tickner *et al.* 2000; Rabeni *et al.* 2002). As summarised by Buffagni *et al.* (2000), habitats that are recognisable from simple visual survey are termed 'potential habitats'. Where the numerical analysis of the faunal assemblages of these habitats produces an objective classification of habitats which support different assemblages, these are then regarded as 'functional habitats'. Although their definition is based in structural aspects of the fauna, the term functional habitats recognises how important the presence or absence of the various functional habitats might be for river processes, ecological 'health' and diversity of biota (Buffagni *et al.* 2000).

The FHC is based on the premise that it is possible to manage habitats in rivers far more easily than it is to manage species (Armitage & Pardo 1995; Buffagni *et al.* 2000; Kemp *et al.* 2000; Tickner *et al.* 2000), particularly in species-rich systems, and those where little is known of the life history or ecological requirements of individual species (Armitage & Pardo 1995). Since its development, the FHC has gained acceptance and has been widely employed in the Northern Hemisphere, i) to more clearly detect the effects of lowland river regulation in preference to more conventional biological assessment techniques (Armitage & Pardo 1995), ii) as a basis to establish cost-effective monitoring programs for improved river management (Buffagni *et al.* 2000; Troia & Gido 2013), iii) to maximise habitat heterogeneity and therefore biodiversity in river rehabilitation projects (Moulton *et al.* 2007; Suen & Su 2010), and iv) in the assessment of the impact of flow reduction on lotic fauna (Brunke *et al.* 2001; Vezza *et al.* 2012). Because river habitats are influenced by geomorphological processes (Harper & Everard 1998), they are sensitive to anthropogenic disturbance, such as flow regulation, and thus are an important focus for river management (Armitage *et al.* 2001). Indeed, from a management perspective, flow-related changes in habitat distribution and extent are more easily discerned than changes in the distribution, abundance and biomass of species based on infrequent sampling of populations. If flow volume, duration and frequency are sufficient to conserve diversity of in-stream habitats, then the corollary is that aquatic biodiversity also will be protected.

The FHC has been mainly tested on macroinvertebrate assemblages of European rivers (Armitage & Pardo 1995; Buffagni *et al.* 2000; Kemp *et al.* 2000; Brunke *et al.* 2001), with few instances of it being applied to fish assemblages (Copp 1991; Harper & Everard 1998; Kemp *et al.* 1999; Carl 2000; Crook *et al.* 2001). Prior to its application to the Ord River (Storey & Lynas 2007), the FHC had not been applied in Australia, although habitat associations have been studied (see Boys & Thoms 2006; Kennard *et al.* 2006; Rayner *et al.* 2008). The efficacy of this tool in river management in Australia will largely depend on the presence of discrete, easily recognisable physical habitats that support distinct suites of species (*sensu* functional habitats; Armitage & Pardo 1995; Pardo & Armitage 1997; Kemp *et al.* 1999, 2000; Buffagni *et al.* 2000; White & Irvine 2003).

The Ord River, in the remote north of Western Australia presented an opportunity to trial the FHC. Currently, approximately 90% of the catchment area is impounded to provide water for irrigated agriculture and for the generation of hydroelectric power. There are plans to more than double the area under irrigation, which could triple water demand. If this increased demand were to be met, it would mean a reduction in the amount of water for the environment (Storey & Trayler 2006). The State agency responsible for river management was tasked with developing an environmental flow for the river, but with little understanding of its ecology (Trayler *et al.* 2002; Storey & Trayler 2006). Preliminary surveys revealed a diverse macroinvertebrate and fish fauna, with many undescribed macroinvertebrate species, and a paucity of ecological or life history information for fish and macroinvertebrates (Storey & Trayler 2006). Therefore, the FHC was seen as a means to manage this system. The aim of this study was to test whether the underlying tenets of the FHC apply to fish assemblages of the LOR, namely: 1) do easily recognisable habitats exist within the system?; 2) do they support distinct fish assemblages?

This is the second of two studies on the application of the FHC to management of the Ord River, the first demonstrating concordance between macroinvertebrate fauna and habitat types (Storey & Lynas 2007).

METHODS

Study Area

The Ord River, located in the Northern Province (Unmack 2013) of the Kimberley region of Western Australia (Figure 1), is one of the state's major river systems, around 650 km long, with a catchment area of 46,100 km². The climate is semi-arid to arid monsoonal with two distinct seasons: a warm, dry season (May to October) and a hot, wet season (November to April). Monsoonal depressions and tropical cyclones are responsible for the vast majority of annual rainfall (ca. 870 mm per annum at Kununurra), with 90% falling during the wet season (Trayler *et al.* 2002).
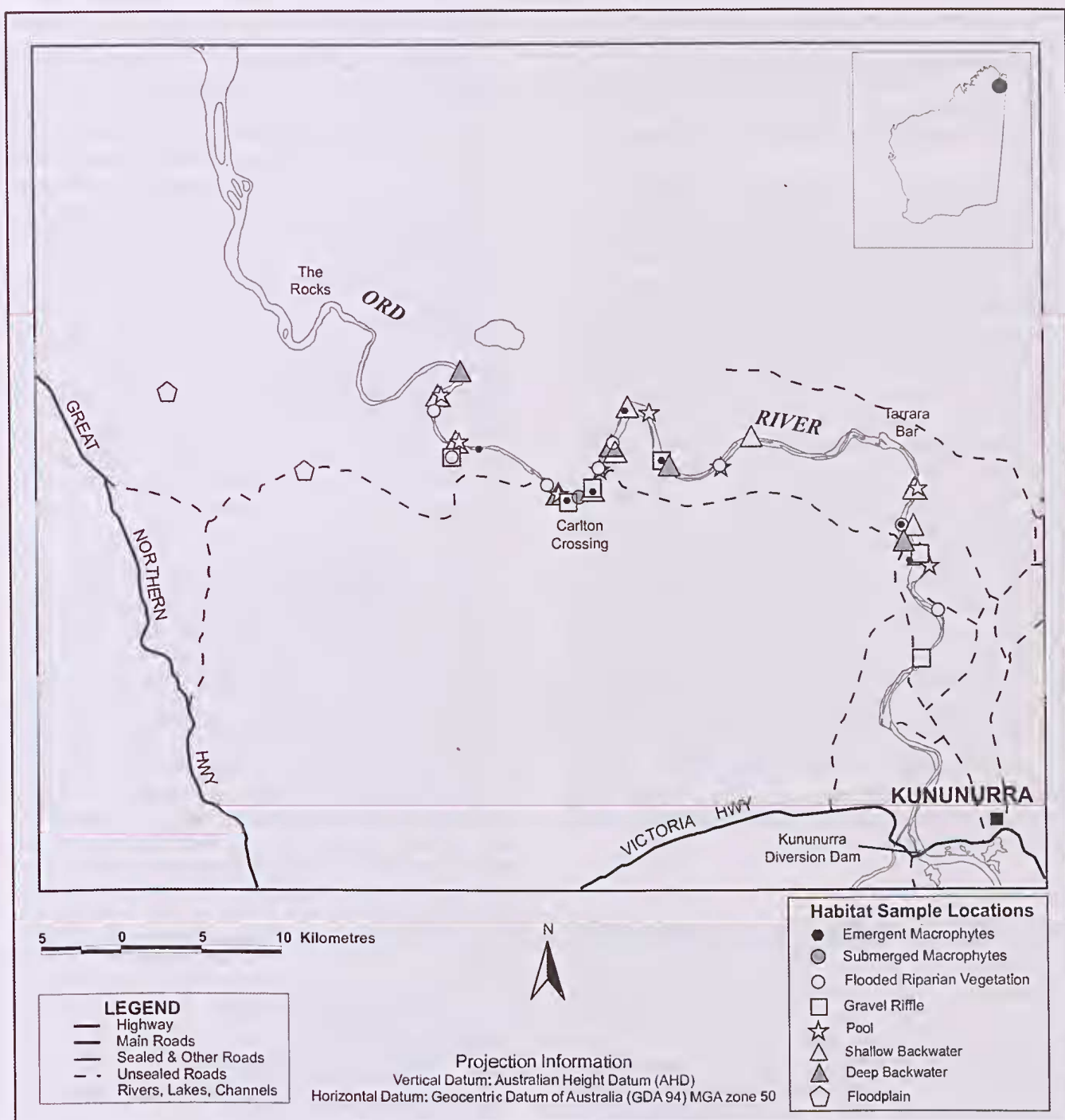
Figure 1 Location of habitats sampled on the Lower Ord River, Western Australia.

The Ord River is impounded by the 13.7 m high Kununurra Diversion Dam (KDD), which forms Lake Kununurra, and the 98.5 m high Ord River Dam (ORD) a further 55 km upstream, which forms the much larger Lake Argyle (surface area 74 000 ha, storage 10 700 GL). Water is released via the ORD into Lake Kununurra to provide a hydraulic head to feed water to irrigation paddocks. Water is then released from the KDD to maintain flows in the river downstream of the dams; the Lower Ord River (LOR). Regulation has transformed the system from a seasonally-flowing to a permanently-flowing river. Wet season peak flows are much reduced, but there is now constant flow during the dry season. As

a result the system supports a greater abundance of fish, birds and crocodiles than would historically have been present (Storey & Trayler 2006). Small but important recreational and commercial fisheries have developed subsequent to regulation, as has the listing of two Ramsar wetlands of international importance. The greatest effect of increased irrigation will be a decrease in mean dry season flows, from the current ca. 80 m^3 sec^{-1} to ca. 40–45 m^3 sec^{-1}. This will result in an approximate 50 cm drop in current late dry season water levels. Modelling indicates that reduced discharge is likely to change the proportion of shallow to deep water habitats in the low-flow dry season, particularly the area of habitats along margins

and shallows, as well as the rapids/gravel runs. However, there will be little effect on current wet season flows which are determined by high intensity monsoonal and cyclonic rains and the seasonally flowing, but unregulated Dunham River which enters the LOR below the KDD, providing wet season high flows (Trayler *et al.* 2002).

Sampling in the current study was conducted along the LOR, a meandering 70 km lowland section between the KDD and the Ord River estuary. The dry season channel is approximately 150 m wide with pools up to 5 m deep. Approximately 80% of the LOR consists of long pools (each 2–3 km in length), interspersed by rock bar/boulder rapids and gravel/cobble runs. These large pools are lined by a diversity of habitats, including shallow submerged macrophyte beds (predominantly *Vallisnaria americana* Michaux), beds of emergent reeds/rushes (*Phragmites australis* (Cav) Trin. Ex Steud, *Typha domingensis* Pers) adjacent to deeper banks, shallow backwaters, and shorelines of sand and silt. Riparian vegetation along the shoreline consists of a mixture of silver cadjeput, *Melaleuca argentea* W. Fitz., cadjeput *Melaleuca leucadendra* (L.) L., river gum *Eucalyptus camaldulensis* Denh, freshwater mangroves *Barringtonia angulata* (L.) Gaertn., white dragon tree *Sesbania formosa* F. Muell., and pandanus palms *Pandanus aquaticus* R. Br (Doupé & Pettit 2002). The river supports regionally diverse fish (~ 30 species) and macroinvertebrate (~ 170 species) faunas (Storey & Trayler 2006), and waterbird fauna (115 species of resident and migratory waterbirds and shorebirds) (Burbidge *et al.* 1991; Halse *et al.* 1996). It also supports large populations of the predominantly piscivorous freshwater crocodile *Crocodilus johnstoni* Krefft, but also the aggressive, potentially human-eating estuarine species *Crocodilus porosus* Schneider. Both species are protected.

Field sampling

Sampling was conducted in the late dry season (16th–26th October 2001), when conditions were hot (39–43 °C) and humid, with occasional isolated thunderstorms. Sampling was then repeated in the late wet season (15th–24th April 2002), when seasonal rains had finished and air temperatures were approximately 35 °C, but river levels were still elevated. Although not gauged, discharge on each sampling occasion was constant over the sampling period, with depth changing < 10 cm. To minimise spatial bias, the LOR was divided into lower (Carlton Crossing to The Rocks), middle (Tarrara Bar to Carlton Crossing) and upper (KDD to Tarrara Bar) reaches and replicate samples of each habitat stratified across all three reaches in each season (Figure 1). Logistical constraints such as daily travel time by boat from field camps, and limited boat access to some reaches due to impassable rapids and no road access, meant that sampling sites were not evenly distributed along the length of the reach. Due to the high risk of attack from estuarine crocodiles, sampling was conducted predominantly from a boat.

Eight visually discernible 'potential' habitat types were identified, grouped into two broad categories: i) deep water habitats (≥ 1 m); deep backwaters, river pools, deep water adjacent to stands of emergent macrophyte (*Phragmites australis*) and flooded riparian

vegetation along the margins and on low benches, and ii) shallow water habitats (< 1 m); shallow backwaters, submerged macrophyte beds, gravel-cobble runs and floodplain lagoons. To test whether these visually identifiable habitats represented discrete habitat types, a range of environmental variables were measured at each replicate site (Table 1). Physico-chemical variables were measured *in situ* using a Yeo-Kal Model 611 multiprobe water quality analyser. Water velocity was measured with a Marsh-McBirney velocity meter at approximately 0.6 of water depth. Water depth was measured at 10 randomly selected locations within each site with a graduated staff (< 1.5 m) or a Garmin Model 135 GPSMAP sounder (> 1.5 m), and location of sites recorded with the Garmin GPS. Percent cover of different substrate and vegetation types were estimated visually (where water clarity allowed), or estimated by 'sounding' the bottom with a plumb line. To limit variation due to different observers, all estimations were made by the same sampler. As an indication of habitat heterogeneity, the number of organic and inorganic substrate types represented at each site was totalled.

To test whether these 'potential' habitats supported distinct fish assemblages, fish were sampled from each replicate habitat using two standard methods. These methods have been employed extensively throughout the Northern Province (Bishop *et al.* 1986, 1990; Larson 1999, WRC 2003; Storey unpub. data) to provide as representative sample as possible of communities in deep and shallow water habitats. All deep water habitats (pools, deep backwaters, emergent macrophyte beds and flooded riparian vegetation) were sampled using multi-panel gill nets (30 m long, consisting of six panels, each 5 m in length with a 2 m drop and stretched mesh size increasing in ~ 2.5 cm increments from 2.5 to 15 cm). For each replicate sample, two gill nets were set for 3 h (either from 0800 to 1100 h, or from 1400 to 1700 h). Nets were set 50 m apart, angled at 30–45 degrees to the bank (depending upon strength of flow), with smallest mesh size attached to the bank. In addition, two replicate longlines (20 m long, with 12 hooks on each line (Mustad Tuna Circle size 11/0 on 30 kg traces), baited with fresh fish) were set for the same period as the gill nets. Nets and lines were recovered at the end of the set period and all fish removed and catch by both methods combined. Gill nets were not effective in sampling shallow water habitats, therefore, a beach seine (20 m long x 1.5 m deep) constructed from 10 mm diamond mesh was used. It was not possible to conduct seine netting in deep water habitats. Seining at shallow water habitats was standardised either by drawing the seine through the whole habitat (i.e. small, shallow backwaters), or by walking the seine perpendicular to the shore and encircling a set area of habitat. Samplers carried a tape measure and paced the distance thereby sampling 20 m² of each habitat. Longlines were also set in each shallow water habitat, as per above. Longlines were recovered at the end of the set period and catch by both methods combined. All fish caught were identified to species, principally following the taxonomy of Allen (1989) and Allen *et al.* (2002), weighed and fork length (FL; snout to fork of tail or snout to posterior margin of tail if the caudal fin was not forked) recorded before being released. Where large numbers of small species were taken, a random sub-sample of at least 10 specimens

Table 1 Measured and derived environmental variables.

Variable	Code
Temperature (°C)	temp
pH (H⁺)	pH
Dissolved oxygen (% saturation)	DO%
Dissolved oxygen (mg L⁻¹)	DO mg/L
Conductivity (mS cm⁻¹)	EC
Salinity (mg L⁻¹)	sal
Turbidity (NTU	turb
Redox potential (mV)	redox
Velocity (cms sec⁻¹)	vel
Mean depth (cm)	depM
Variance in depth (cm)	depV
Mineral substrates (total % cover within habitat) [1]	min
Bedrock (% cover)	bedr
Boulders >256 mm (% cover)	boul
Cobbles 64–256 mm (% cover)	cobb
Pebbles 16–64 mm (% cover)	pebb
Gravel 4–16 mm (% cover)	grav
Sand 1–4 mm (% cover)	sand
Silt <1 mm (% cover)	silt
Emergent macrophyte (% cover within habitat)	emerg
Submerged macrophyte (% cover within habitat)	submerg
Floating macrophyte (% cover within habitat)	float
Algae (% cover within habitat)	algae
Detritus (% cover within habitat)	detr
Riparian vegetation (% cover within habitat)	ripvegco
Large woody debris (>10 cm diameter) (% cover within habitat)	LWD
Root mats (% cover within habitat)	rootm
Riparian vegetation (% cover within habitat)	ripveg
Snag (<10 cm diameter) density (1–3; 1 = sparse, 3 = dense)	snag
Habitat complexity (total number of substrate types present)	complx
Bank angle (degree)	bkang
Undercuts (% cover within habitat)	underc
Substrate compaction (1 = loose array, 5 = armoured, tightly packed)	compct

[1] Mineral substrates and substrate surface areas were estimated visually in shallow water or by 'sounding' the bottom with a lead weight in deeper water.

were individually weighed and measured and the remainder counted and a total weight recorded.

Where present, two replicates of each habitat were sampled within each reach during each season, providing a maximum of six replicates per habitat in any season. During the late wet season, water levels in the main channel were at least 3 m higher than during the late dry season. As a result, the distribution of habitats changed and not all habitats were present in both seasons. In the dry season, lower water levels meant that floodplain habitats were dry, deep backwaters did not exist, and flooded riparian zones were restricted to a narrow margin along the shore. In the wet season, higher water levels meant that shallow backwaters became deep backwaters, the floodplain was inundated and so could be sampled, and broad, low benches vegetated with silver cadjeput, cadjeput, freshwater mangroves, white dragon tree and pandanus became broad areas of flooded riparian habitat. Gravel-cobble runs and submerged macrophyte beds were not accessible due to deep, turbid water over these habitats in the wet season. Though there

was some seasonal tidal influence in the most downstream part of the study area (The Rocks), all reaches surveyed were freshwater.

Data analysis

Amongst habitat differences in environmental variables and fish species richness were investigated by two-way ANOVA, by habitat and season (IBM SPSS Statistics v19). The potential confounding influence of different sampling methods is here acknowledged, particularly how abundance of fish caught may bias the number of species collected (Gotelli & Colwell, 2001). Therefore, species richness data were re-estimated using rarefaction, performed using PRIMER (v6) software package (Clarke & Gorley 2006). The assumptions of normality and homogeneity of sample variances were checked using Shapiro-Wilk (Shapiro & Wilk 1965) and Levene's (Levene 1960) tests, respectively. Environmental data were $\log_{10}(x+1)$ transformed or arcsine transformed (percent data), where appropriate. Where multiple tests on environmental variables were performed, a

Bonferroni correction was applied to minimise the chance of Type I errors, whereby critical p = (0.05/n), where n = number of tests performed. Tukey's HSD multiple range test was used to locate between-habitat differences where there was a significant main effect.

Multivariate patterns in environmental and fish presence/absence data were analysed using procedures from the PRIMER (v6) software package (Clarke & Gorley 2006). The permutational multivariate analysis of variance (PERMANOVA) add-on to PRIMER v6 was used to test for significant (p < 0.05) habitat effects on environmental variables or fish species assemblages (Anderson 2001a, b; McArdle & Anderson 2001; Anderson *et al*. 2008). Non-metric Multi-Dimensional Scaling (nMDS) ordination plots (Clarke & Warwick 2001) were constructed to visualise differences between habitats. nMDS ordinations were based on Euclidean distance measures for environmental data, and Bray-Curtis similarity measures for fish presence/absence data. Ordinations were depicted as two-dimensional plots.

In recognition that different life stages within a species, particularly for fish, have different habitat requirements (Harris & Kangas 1988; Cowx & Welcomme 1998), prior to analysis species were divided into 'pseudospecies' based on size classes. A maximum of three size classes were recognised per species, corresponding approximately to juveniles, sub-adults and adults as determined from the literature (Allen 1982; Bishop *et al*. 2001; Allen *et al*. 2002). Analyses were performed to test between individual habitat types and between deep and shallow water habitats.

Habitat preferences of pseudospecies were examined using both chi-squared (χ^2) tests and the similarity percentage analysis (SIMPER) within PRIMER, both of which assess species occurrences across habitats. The χ^2 test was applied only to those pseudospecies with sufficient levels of occurrence within and across habitats to allow valid analysis, as determined by the statistical package. Analyses were significant if p < 0.05, and within a pseudospecies, habitats with the greatest deviation of the observed from the expected frequency were taken to indicate a preference of the pseudospecies for that habitat type.

Distance-based linear models (DISTLM) were used to explore multivariate relationships between environmental variables (Table 1) and assemblage data using pseudospecies (Anderson 2001a, 2002; McArdle & Anderson 2001). The final multivariate multiple regression model that best explained the variation in the species data was chosen using the stepwise forward-selection procedure and AIC selection criterion. Significance of regression relationships was assessed using 9999 random permutations of the data.

RESULTS

Environmental descriptors of habitats

Significant between-habitat and -season differences were detected for 15 and 5 of the environmental variables, respectively (ANOVA, Table 2). Most measures of water quality showed little spatial variability, indicating waters were well mixed both vertically and laterally across all habitat types. The exceptions were lower pH and higher temperature in floodplain habitat, resultant of shallow, standing waters and soils rich in organics. Significant spatial differences were identified for velocity, depth, bank angle, habitat complexity (e.g. % mineral substrate, pebbles, silt, snags), and vegetation cover (e.g. emergent/submerged/floating macrophytes, algae, root mats and trailing riparian vegetation). Many of these habitat differences reflected the readily observed physical

Table 2 Results from two-way ANOVA and Tukey's *post hoc* test on environmental variables measured over two seasons (W = late wet; D = late dry) across eight habitat types (B = shallow backwater; DB = deep backwater; E = emergent macrophyte; F = flooded riparian vegetation; FP = floodplain; G = gravel-cobble run; P = pool; SM = submerged macrophyte). Only variables for which there was at least one significant main effect are shown here (p <0.05). Habitats or seasons joined by a common line are not significantly different (Bonferroni adjusted p value <0.002). Arithmetic means (+ 1 SE in parentheses) are presented for each habitat/season.

Habitat variable	Habitat (df =7)		Season (df =1)		Interaction (df =3)		Pairwise comparison										
	F	p	F	p	F	p	Habitat (Tukey's HSD multiple comparison test)								Season	
pH	3.40	0.00	22.10	<0.0001	0.69	>0.05	DB	P	F	E	SM	B	G	FP	W	D
							8.5	8.3	8.1	8.1	8.0	8.0	7.7	6.9	8.2	7.8
							(0.19)	(0.18)	(0.14)	(0.19)	(0)	(0.20)	(0.24)	(0.26)	(0.19)	(0.18)
Turbidity	1.63	>0.05	21.58	<0.0001	0.87	>0.05	SM	B	G	F	E	P	FP	DB	D	W
							20.7	14.6	15.6	14.9	14.3	12.8	10.6	9.8	17.9	11.4
							(0)	(1.82)	(2.34)	(1.63)	(1.68)	(1.32)	(5.55)	(0.66)	(1.92)	(1.97)
Temp	2.60	0.0231	0.08	>0.05	0.22	>0.05	FP	SM	DB	E	B	P	F	G	W	D
							33.1	30.7	30.6	30.4	30.3	30.1	30.1	30.0	30.7	30.3
							(2.12)	(0)	(0.23)	(0.27)	(0.51)	(0.32)	(0.27)	(0.39)	(0.58)	(0.40)
Velocity	15.04	<0.0001	1.23	>0.05	3.78	0.0162	G	E	P	F	DB	SM	B	FP	D	W
							56.1	26.9	25.2	9.4	7.8	3.0	0	0	18.8	12.9
							(0.20)	(4.90)	(5.45)	(2.95)	(4.50)	(0)	(0)	(0)	(5.14)	(2.60)

Table 2 (cont.)

Habitat variable	Habitat (df=7)		Season (df=1)		Interaction (df=3)		Pairwise comparison								Season	
	F	p	F	p	F	p	Habitat (Tukey's HSD multiple comparison test)									
Depth	24.61	<0.0001	0.01	>0.05	15.39	<0.0001	P 3.6 (0.29)	E 2.4 (0.38)	DB 2.2 (0.28)	F 2.2 (0.29)	SM 0.9 (0)	B 0.5 (0.08)	G 0.5 (0.08)	FP 0.4 (0.16)	D 1.7 (1.24)	W 1.9 (1.22)
%Pebble	25.14	<0.0001	3.65	>0.05	1.91	>0.05	G 63.3 (5.70)	E 7.1 (3.45)	F 4.8 (2.85)	P 4.7 (4.65)	B 0.2 (0.15)	FP 0 (0)	DB 0 (0)	SM 0 (0)	D 15.1 (4.38)	W 1.0 (1.0)
%Sand	2.44	0.0313	1.34	>0.05	0.64	>0.05	B 41.5 (13.30)	E 40.4 (6.60)	P 36.0 (14.35)	F 17.9 (10.95)	DB 11.7 (0.0)	G 6.2 (0.80)	FP 0 (0)	SM 0 (0)	W 24.1 (5.71)	D 23.5 (6.58)
%Silt	4.90	0.0003	3.81	>0.05	2.58	>0.05	FP 100 (0)	SM 100 (0)	DB 88.3 (8.30)	F 68.4 (13.75)	B 56.4 (13.90)	P 45.0 (15.65)	E 28.8 (3.30)	G 0.5 (0.50)	W 70.0 (7.75)	D 44.3 (11.10)
%Mineral	14.53	<0.0001	0.78	>0.05	1.70	>0.05	G 100 (0)	P 78.0 (9.55)	DB 77.2 (5.60)	B 76.8 (10.60)	E 38.6 (4.70)	F 34.7 (6.50)	SM 18.0 (0)	FP 4.0 (4.0)	D 59.3 (4.54)	W 49.8 (8.27)
%Emergent veg.	61.81	<0.0001	0.91	>0.05	2.05	>0.05	E 56.3 (2.70)	FP 30.0 (30.0)	DB 4.2 (2.0)	B 2.1 (1.70)	F 1.7 (1.25)	P 0.5 (0.50)	G 0 (0)	SM 0 (0)	W 15.0 (6.07)	D 10.8 (1.58)
%Submerged veg.	11.74	<0.0001	0.38	>0.05	0.39	>0.05	SM 75.0 (0)	FP 50.0 (40.0)	B 10.1 (6.75)	DB 0.8 (0.80)	E 0 (0)	G 0 (0)	F 0 (0)	P 0 (0)	D 13.5 (0.98)	W 10.8 (8.23)
%Floating	58.79	<0.0001	0.00	>0.05	0.00	>0.05	FP 15 (5.0)	B 0 (0)	E 0 (0)	DB 0 (0)	G 0 (0)	P 0 (0)	F 0 (0)	SM 0 (0)	W 2.5 (0.83)	D 0 (0)
%Algal cover	6.53	<0.0001	0.00	>0.05	0.00	>0.05	FP 0.5 (0.5)	B 0 (0)	E 0 (0)	DB 0 (0)	G 0 (0)	P 0 (0)	F 0 (0)	SM 0 (0)	W 0.1 (0.08)	D 0 (0)
%Detritus	3.09	0.0088	0.53	>0.05	1.13	>0.05	B 8.0 (3.30)	F 5.1 (1.40)	SM 5.0 (0.0)	DB 2.5 (1.10)	E 1.9 (1.15)	P 1.1 (0.40)	FP 0 (0.50)	G 0 (0)	W 3. (1.36)	D 2.6 (0.59)
%Trailing	5.18	0.0002	46.40	<0.0001	5.08	0.0038	D 5.8 (0.83)	F 4.0 (0.73)	P 2.3 (0.39)	B 1.4 (0.84)	E 0.6 (0.49)	FP 0 (0)	G 0 (0)	S 0 (0)	W 3.6 (0.87)	D 0.1 (0.10)
%Root mat	9.94	<0.0001	4.11	0.0480	1.12	>0.05	F 5.0 (0.75)	DB 3.7 (0.80)	P 3.4 (0.65)	E 0.5 (0.5)	B 0.1 (0.1)	FP 0 (0)	G 0 (0)	SM 0 (0)	W 2.4 (0.37)	D 1.1 (0.52)
%Riparian vege. cover	11.39	<0.0001	27.14	<0.0001	8.56	0.0001	F 42.1 (6.60)	DB 11.0 (2.90)	B 9.9 (5.90)	P 8.6 (3.35)	E 8.5 (4.45)	SM 5.0 (0)	FP 2.5 (2.50)	G 0.8 (0.80)	W 20.1 (5.75)	D 6.1 (2.46)
%Snags	16.88	<0.0001	0.78	>0.05	0.75	>0.05	F 2.1 (0.29)	P 1.2 (0.12)	DB 1.2 (0.31)	SM 1.0 (0)	E 0.7 (0.21)	B 0.2 (0.17)	G 0 (0)	FP 0 (0)	W 0.9 (0.20)	D 0.8 (0.14)
Habitat complexity	17.53	<0.0001	0.05	>0.05	0.46	>0.05	F 1.9 (0.22)	P 1.8 (0.19)	SM 1.0 (0)	DB 1.0 (0.26)	E 0.9 (0.33)	B 0.2 (0.17)	G 0 (0)	FP 0 (0)	W 1.0 (0.19)	D 1.0 (0.19)
Bank angle (degrees)	11.20	<0.0001	26.70	<0.0001	4.08	0.0115	P 58.4 (6.10)	DM 43.3 (10.1)	F 41.7 (5.55)	E 40.4 (10.25)	SM 35.0 (0)	B 17.1 (2.65)	G 11.7 (1.70)	FP 5.0 (0)	D 42.2 (4.12)	W 26.1 (6.72)

(a) Late dry season

2D Stress: 0.17

(b) Late wet season

2D Stress: 0.16
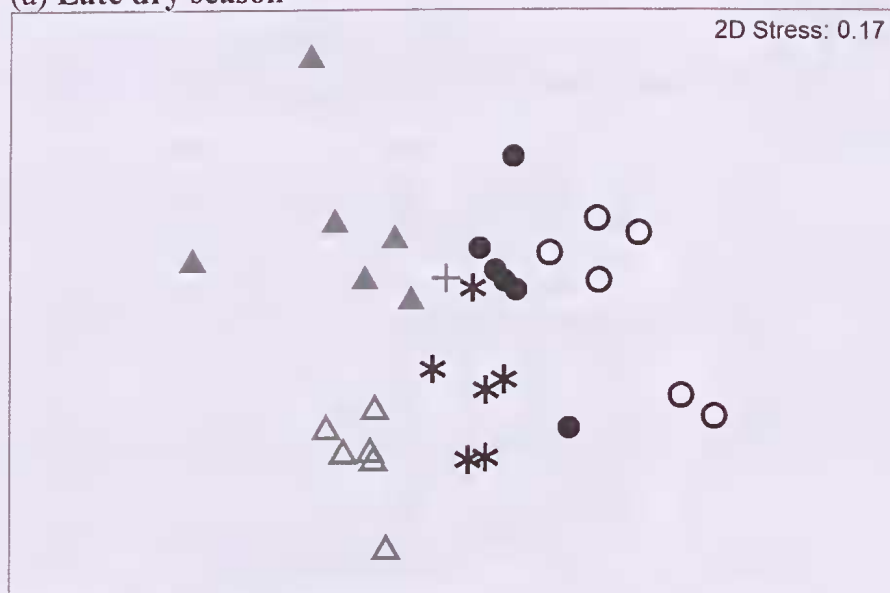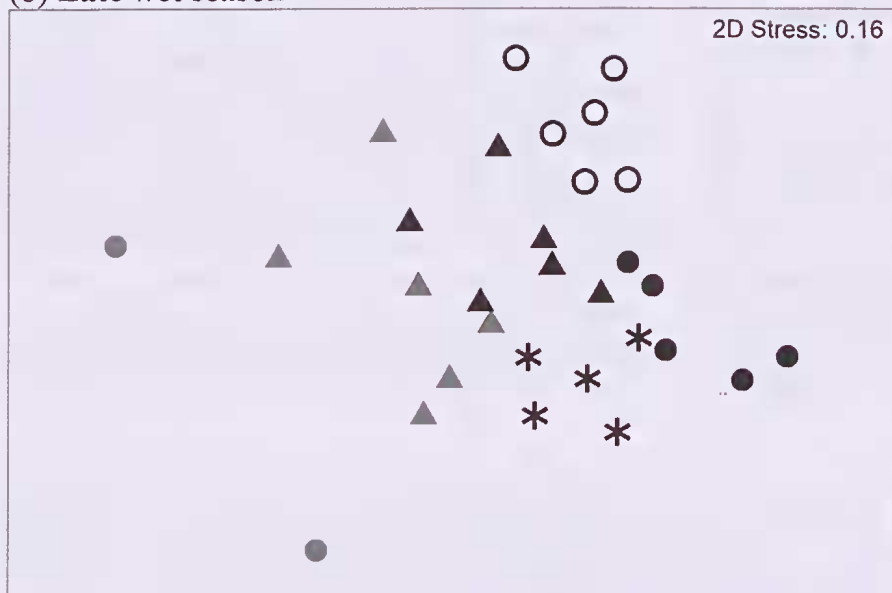
▲ deep backwater,
● pool,
○ flooded riparian vegetation,
✳ emergent macrophyte,
▲ shallow backwater,
▦ floodplain,
▽ gravel-cobble run,
+ submerged macrophyte

Figure 2 Unconstrained nMDS ordination plots, comparing environmental variables among habitats for each season on the basis of Euclidean distance measure.

differences that were used to visually define habitats. Interaction terms were significant for mean water depth and % riparian vegetation cover reflecting that changes in depth and cover were not consistent across habitats and between seasons (i.e. shallow backwaters moved laterally in the wet season to the edges of flooded benches which were well vegetated, therefore cover increased in the wet season, but depth stayed the same as in the dry season), but also that not all habitats were represented in each season. Seasonal differences reflected increasing depth and velocity during the wet season, with redistribution of habitats. For example, submerged macrophyte beds and gravel-cobble runs were drowned-out and therefore not accessible, previously shallow backwaters became deep backwaters, and new areas of shallow water appeared at the channel edge, often within or behind the margin of riparian vegetation.

There was a significant difference in environmental parameters between deep and shallow water habitats in both seasons as determined by PERMANOVA (Table 3). Within each season, pairwise comparison of each habitat type indicated significant separation of most habitats. In the dry season, habitats were significantly different from each other, with the exception of submerged macrophytes, which could not be differentiated from any other habitat owing to no replication of this habitat. Deep and shallow water habitats were the most distinctive in the dry as shown in the unconstrained ordination plots (nMDS, Figure 2a–b).

Fish assemblages within habitats

Sampling across all habitats in both seasons recorded 3 763 fish, representing 38 species from 28 families (Appendix). The majority of species were distributed throughout all three reaches of the LOR, with the exception of six species that are either 'marine or

Table 3 Results from (a) two-way PERMANOVA testing for season or habitat effects on the suite of environmental variables, based on Euclidean distance measure, and (b) pairwise comparisons for habitat effects within each season using permutations of the t-statistic. Significance level p(perm) <0.05; significant results for pairwise comparisons are indicated as, <0.05*, <0.01**. *NA* = not available; not all habitats were present in both seasons. Refer Table 2 for habitat codes.

(a) Main test	Habitat (df =7)				Season (df =1)				Interaction (df =3)			
	SS	MSS	F	p(perm)	SS	MS	F	p(perm)	SS	MS	F	p(perm)
Environmental variables	643	92	6.320	0.0001	130	130	8.928	0.0001	74	25	1.695	0.009

(b)	Pairwise comparisons for habitat									
	Late dry season					Late wet season				
	B	E	F	G	P	B	E	F	P	DB
E	2.223**					1.907**				
F	2.647**	2.267**				2.492**	3.136**			
G	2.884**	2.535**	3.237**			*NA*	*NA*	*NA*		
P	2.218**	2.155**	1.840**	3.272**		2.128	1.513**	2.518**		
SM	1.303	1.582	1.455	2.247	1.777	*NA*	*NA*	*NA*	*NA*	
DB	*NA*	*NA*	*NA*	*NA*	*NA*	1.669	1.882**	2.154**	1.453*	
FP	*NA*	*NA*	*NA*	*NA*	*NA*	1.480	2.042*	2.489**	2.120*	1.846*

Table 4 Results from two-way ANOVA and Tukey's *post hoc* testing for season (D = late dry; W = late wet) or habitat effects on fish species richness. Habitats or seasons joined by a common line are not significantly different (p value <0.05). Arithmetic means (+ 1 SE in parentheses) for species richness are presented for each habitat. Refer Table 2 for habitat codes.

Species variable	Habitat (df =7)		Season (df =1)		Interaction (df =3)		Pairwise comparison									
	F	p	F	p	F	p	Habitat (Tukey's HSD multiple comparison test)								Season	
Richness (no. of species)	2.73	0.023	0.01	0.987	3.83	0.015	SM 7.53 (0)	DB 6.3 (0.70)	F 6.2 (0.49)	B 5.8 (0.49)	P 5.8 (0.65)	E 5.3 (0.52)	FP 4.5 (1.2)	G 2.9 (0.70)	D 5.7 (0.34)	W 5.2 (0.31)

estuarine vagrants' or 'marine migrants' and which were only occasionally caught in the lower tidally-influenced reach, including *Elops hawaiensis* Regan, *Arrhamphus sclerolepis sclerolepis* Günther, *Sciades leptaspis* (Bleeker), *Marilyna meraukensis* (de Beaufort), *Thryssa* sp. and Mugilidae spp.

There were significant between-habitat differences in species richness, but no significant seasonal effect (Table 4). Fish species richness was ~ 60% less in gravel-cobble runs and floodplain habitats than in submerged macrophyte and shallow backwater habitats (Figure 3). This was primarily due to the presence of many juvenile and small-bodied fish species in these latter habitats.

Fish assemblages differed significantly between habitats (PERMANOVA, Table 5a). In the dry season, pairwise comparisons indicated the majority of habitats were significantly different with the exception of flooded riparian vegetation compared with emergent macrophyte beds and pools, and all comparisons with submerged macrophyte beds, reflecting small sample size of the

latter (Table 5b). In the wet season most habitats were different from each other, except deep backwaters, pools and emergent macrophytes compared with each other (Table 5b). The nMDS ordinations on assemblages did not clearly distinguish individual habitats, but did show a general separation of shallow from deep water habitats in both seasons (Figure 4a–b).

SIMPER analyses revealed shallow water habitats to be characterised by small-bodied species (e.g. *Ambassis macleayi* (Castelnau), *Amniataba percoides* (Günther), *Glossogobius giuris* (Hamilton) and *Melanotaenia australis* (Castelnau)) and juveniles of large bodied species (*Liza alata* (Steindachner), *Lates calcarifer* (Bloch) and *Nematalosa erebi* (Günther)), while deep water habitats supported more adult and large-bodied fishes (e.g. *L. alata*, *Neoarius graeffei* (Kner & Steindachner), *Neoarius midgleyi* (Kailola & Pierce) and *N. erebi*). Faunal similarity within habitats was low, averaging 33% for deep water and 25% for shallow water habitats. Highest similarity amongst replicates occurred for flooded riparian habitat during

Table 5 Results from (a) two-way PERMANOVA testing for season or habitat effects on fish assemblages based on Bray-Curtis similarity measure, and (b) pairwise comparisons for habitat effects within each season using permutations of the t-statistic. Significance level p(perm) <0.05; significant results for pairwise comparisons are indicated as, <0.05*, <0.01**. NA = not available; not all habitats were present in both seasons. Refer Table 2 for habitat codes.

(a) Main test	Habitat (df =7)				Season (df =1)				Interaction (df =3)			
	SS	MSS	F	p(perm)	SS	MS	F	p(perm)	SS	MS	F	p(perm)
Richness (no. of species)	72258	10323	5.480	0.001	2445	2	1.300	0.23	8069	2690	1.428	0.111

(b)	Pairwise comparisons for habitat											
	Late dry season						Late wet season					
	B	E	F	G	P		B	E	F	P	DB	
E	2.314**						2.892**					
F	3.148**	0.818					3.261**	1.048*				
G	1.617**	1.704**	2.172**				NA	NA	NA			
P	3.148**	1.100*	1.084	2.205**			2.628**	1.878	1.544*			
SM	1.135	1.224	1.930	0.946	2.072		NA	NA	NA	NA		
DB	NA	NA	NA	NA	NA		2.928**	1.067	0.888*	0.917		
FP	NA	NA	NA	NA	NA		1.641*	2.963*	3.598*	2.440*	2.940*	

Table 6 Results of chi-square (χ^2) analysis of associations between eight habitats and 58 fish pseudospecies recorded from the LOR over two consecutive seasons. Only pseudospecies for which there was at least one significant association are shown. Values represent the percentage of samples from each habitats in which each species was recorded, with the number of samples given in parenthesis. Statistical significance of the χ^2 value is given as p. Percentage occurrences highlighted in **bold** indicate preferred habitat(s) of each pseudospecies. Codes for pseudospecies: L = adult, M = sub-adult, S = juvenile. Refer Table 2 for habitat codes.

Pseudospecies	Late dry season							Late wet season						
	B (6)	E (6)	F (6)	G (6)	P (6)	SM (1)	p	B (6)	DB (6)	E (5)	F (6)	FP (2)	P (5)	p
A. macleayi (L)	**33**	0	0	0	0	**100**	0.0076	33	0	0	17	50	0	ns
A. macleayi (M)	17	0	0	0	0	**100**	0.0041	67	0	0	0	**100**	0	0.0003
A. percoides (M)	**67**	0	0	**67**	0	**100**	0.0029	**100**	0	0	0	0	0	<0.0001
A. percoides (S)	**50**	0	0	0	0	0	0.0167	**67**	0	0	0	0	0	0.0014
N. graeffei (L)	0	67	83	33	**100**	**100**	0.0053	0	**100**	80	**100**	0	**100**	0.0004
N. graeffei (M)	0	50	**83**	17	**100**	0	0.0026	0	**83**	60	50	0	**80**	0.0466
N. midgleyi (M)	0	33	67	0	83	0	0.0077	0	17	20	33	0	20	ns
Ambassis sp. (M)	33	0	0	17	0	**100**	0.038	17	0	0	0	0	0	ns
C. ?stercusmuscarum	17	17	0	0	0	**100**	0.0357	17	0	0	0	0	0	ns
G. aprion	17	0	0	0	0	**100**	0.0041	33	0	0	0	0	0	ns
G. giuris	**100**	0	0	17	0	**100**	<0.0001	**67**	0	0	0	0	0	0.0014
H. compressa (L)	0	0	0	0	0	**100**	<0.0001	17	0	0	0	50	0	ns
H. jenkinsi	0	0	0	0	0	**100**	<0.0001	0	17	0	17	0	0	ns
L. alata (L)	67	50	**100**	0	**100**	0	0.0019	33	83	**100**	**100**	0	40	0.019
L. alata (M)	**83**	17	0	17	17	0	0.0184	17	67	20	17	0	0	ns
M. australis (L)	**50**	0	0	17	0	**100**	0.0173	67	0	0	0	**100**	0	0.0003
M. australis (S)	33	0	0	17	0	0	ns	17	0	0	0	**100**	0	0.0005
M. cyprinoides (S)	0	0	0	0	17	**100**	0.0041	17	17	20	0	0	0	ns
N. hyrtlii (L)	0	33	17	0	17	0	ns	0	33	20	67	0	0	0.042
N. erebi (L)	17	17	17	0	50	0	ns	0	83	80	83	0	40	0.0119
N. erebi (M)	17	33	17	0	83	**100**	0.0194	33	50	60	83	0	20	ns
N. erebi (S)	**83**	0	0	33	0	**100**	0.0014	67	33	20	17	0	40	ns
Plotosidae sp. 1	—	—	—	—	—	—	—	0	0	0	0	**100**	0	<0.0001
Plotosidae sp. 2	—	—	—	—	—	—	—	0	0	0	0	50	0	0.0085
P. gulliveri	33	0	0	0	0	**100**	0.0076	—	—	—	—	—	—	—
T. chatareus (L)	33	50	50	0	50	0	ns	17	67	0	83	0	20	0.0103

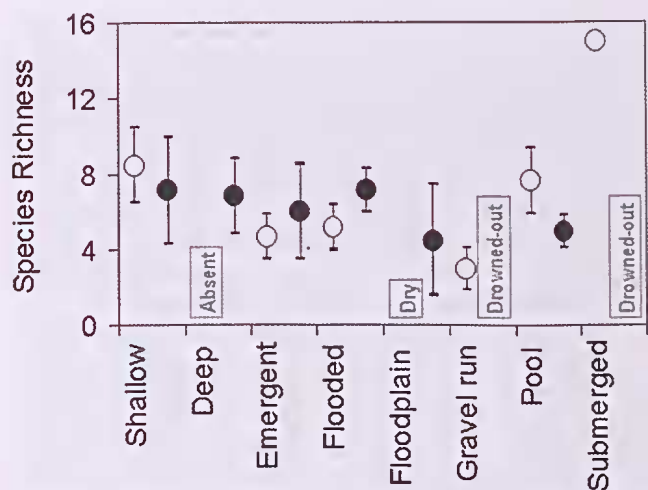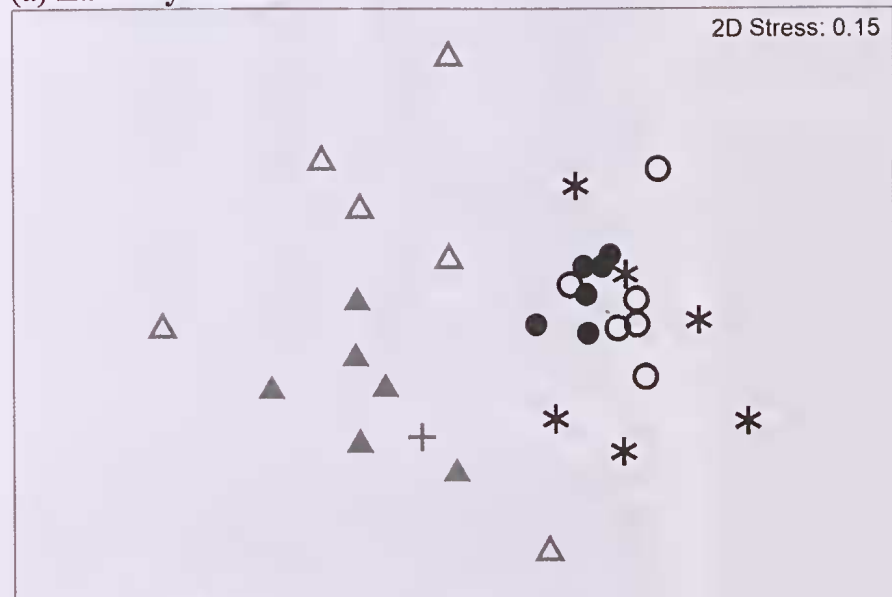**Figure 3** Mean (± 95% confidence interval) species richness of fish in each habitat in each season; O late dry, ● late wet.

the late wet (58%), whilst lowest similarity was within gravel-cobble runs (11%) during the dry.

Frequency analysis (χ^2, Table 6) indicated significant habitat preferences for 42% of pseudospecies present during the dry season and 27% of pseudospecies during the late wet. Of these, the majority favoured shallow backwaters during the dry, but had equal distribution amongst shallow and deep backwaters, floodplain, pool and flooded riparian habitat during the wet season (Figure 5). During the dry season, the shallow backwaters supported higher abundances of *Leiognathus equulus* and *Glossogobius giuris*. Sub-adult *Amniataba percoides* also displayed preference for shallow backwaters and gravel-cobble runs; they were the dominant fish in gravel-cobble runs during the late dry and in shallow backwaters during the late wet season. Floodplain habitat, which was only available during the wet season, was typified by *Ambassis macleayi* and *Melanotaenia australis*. In both seasons, the deeper water

(a) Late dry season

(b) Late wet season

▲ deep backwater,
● pool,
O flooded riparian vegetation,
✳ emergent macrophyte,
▲ shallow backwater,
floodplain,
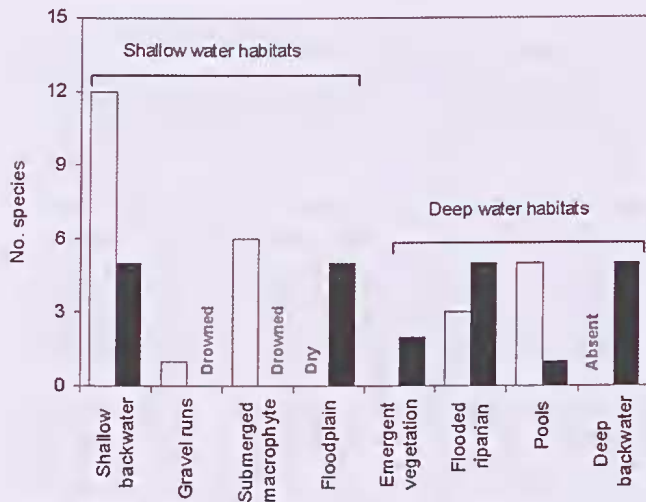gravel-cobble run,
submerged macrophyte
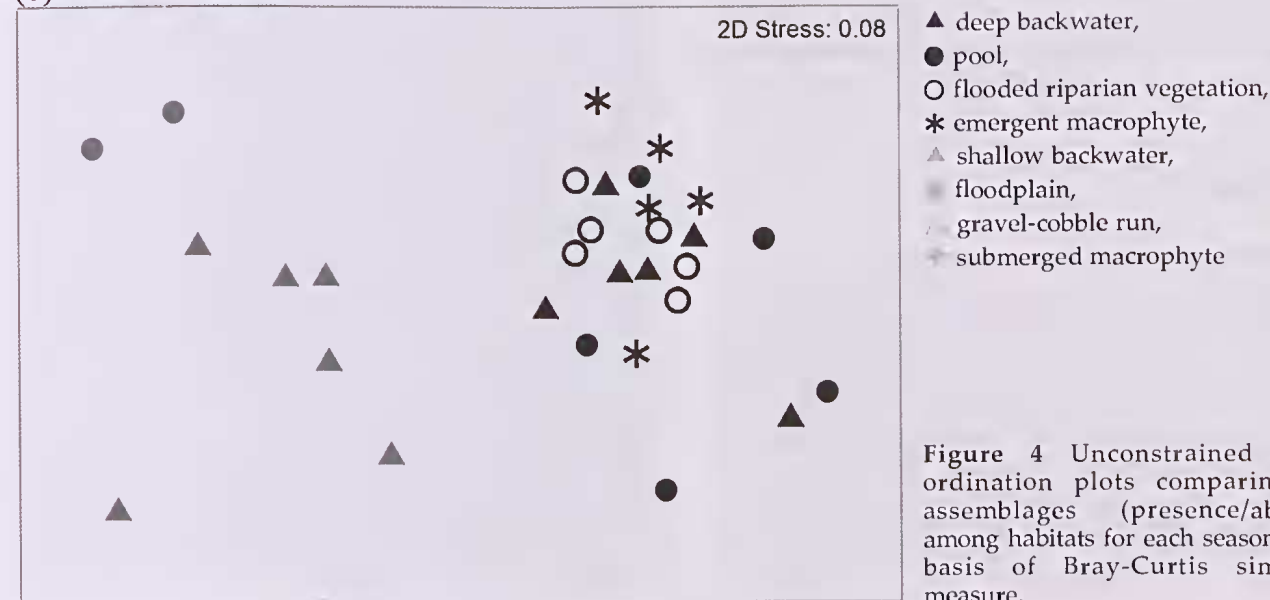
Figure 4 Unconstrained nMDS ordination plots comparing fish assemblages (presence/absence) among habitats for each season on the basis of Bray-Curtis similarity measure.

Figure 5 Number of fish life stages (pseudospecies) showing preferential habitat use in each season; □ late dry season, ■ late wet season, as determined by chi-square contingency table analysis.

habitats were characterised by adult *L. alata* and adult and sub-adult *N. graeffei*.

Multivariate multiple regression analysis identified five environmental variables with significant relationships with fish assemblages during the dry season (Table 7). The variable that individually explained the greatest amount of variation in species presence/absence data was bank angle (24.5%), followed by mean depth (21.9%), habitat complexity (17.2%), % snags (13.9%) and % pebble substrate (9.0%). Of these, stepwise forward selection showed that bank angle and % pebble were the best predictors, together explaining 32.3% of the total variation. In contrast to the dry season, analysis of wet season data identified nine significant environmental variables, three of which were also significant in the dry, i.e. habitat complexity, % snags and mean depth (Table 7). Individual variables that alone explained most variation in species presence/absence data in the wet were habitat complexity (18.2%), mean depth (17.9%), % snags (17.8%), % root mats (16.8%) and % submerged macrophyte (16.7%). The best predictor of species richness in the wet was a combination of four variables (Table 7) that collectively explained 39.4% of the total variation.

DISCUSSION

Evidence for the functional habitat concept

This study demonstrated that visually distinct 'potential' habitats within the LOR could be distinguished on the basis of their physical properties, and these habitats supported different fish assemblages, making them 'functional habitats' *sensu* Armitage & Pardo (1995), Kemp *et al.* (2000), Buffagni *et al.* (2000) and Tickner *et al.* (2000). Eight 'potential' habitats were identified by visual assessment, although not all habitats were present at all times due to seasonal changes in water levels. In the wet season, deep backwaters and floodplain habitats were present due to the higher water levels, but submerged

Table 7 Results of multivariate multiple regression of species presence-absence data on environmental variables. %Var. = percentage of variance in species data explained by the environmental variables individually or through stepwise forward-selection; Cum.% = cumulative percentage of variance explained. Refer Table 1 for environmental variable codes.

	Variable	%Var.	F	p	Cum.%
	Individually				
	bkang	24.5	9.419	0.0001	
	depM	21.9	8.112	0.0001	
Late dry	cmplx	17.2	6.029	0.0001	
	snag	13.9	4.684	0.0006	
	pebb	9.0	2.864	0.0099	
	Fitted stepwise				
	bkang	2	9.419	0.0001	24.5
	pebb		3.224	0.000	32.3
	Individually				
	cmplx	18.2	6.249	0.0001	
	depM	17.9	6.115	0.0003	
	snag	17.8	6.050	0.0002	
	rootm	16.8	5.634	0.0002	
Late wet	subm	16.7	5.600	0.0001	
	pH	11.8	3.760	0.0039	
	vel	10.6	3.419	0.0075	
	cmpct	9.6	3.056	0.0084	
	depV	7.8	2.116	0.0381	
	Fitted stepwise				
	cmplx	18.2	6.249	0.0001	18.2
	subm	8.3	3.067	0.0036	26.6
	depM	7.1	2.796	0.0072	33.7
	rvegco	5.6	2.339	0.0209	39.4

macrophyte beds and gravel-cobble runs were not sampled because they were inundated by deep, fast flowing water and so were not accessible. How these latter habitats function in the wet season is not known, but given their hydrological condition, it seems likely their fish assemblages would be different from the dry season. Submerged macrophyte beds were under-represented in this study (n = 1), but retained in analysis because they are considered a critical habitat. Normally the LOR supports extensive beds of submerged macrophytes, extending in places ~ 30 m into the channel and to a depth of 2–3 m (A. Storey, pers. obs.). Sampling of these beds in subsequent studies showed they provide important habitat for small and juvenile fish, particularly *Glossamia aprion* (Richardson), *Amniataba percoides* and *Hypseleotris compressa* (Kreft), as well as supporting large numbers of *Macrobrachium* prawns and atyid shrimps (A. Storey, unpub. data). However, prolonged flooding in the previous wet season (1:20 rainfall event which resulted in extended over-topping of the ORD) had scoured nearly all of the weed beds from the channel, and at the time of this study they had not re-established. Local fishers reported difficulty in obtaining 'bait fish' (small species and juveniles of larger species) during the dry season in the current study which they attributed to the absence of weed beds, suggesting they were important habitat for these fish.

Types of functional habitats

Analysis of habitats at the broadest level showed deep and shallow water habitats to be functionally distinct. But within these two groups, not all habitats consistently separated on the basis of fish assemblages. In the dry season, shallow backwaters, gravel-cobble runs and pools were most distinct, and in the wet season, floodplain habitat, shallow backwaters, emergent and flooded riparian vegetation were most consistently different from all other habitats. Seasonally, there was greater distinction in terms of physical condition between habitats in the late dry season than the late wet, and a greater number of species showed significant habitat preferences in the dry than the wet season. Four functional habitats could be differentiated in the dry season on the basis of their physical attributes and fish assemblages: shallow backwaters, gravel-cobble runs, channel pools and flooded riparian vegetation. In the wet, emergent macrophyte habitat could also be differentiated, but not channel pools. A relatively small number of physical variables could be used to account for a significant proportion of the variation in species assemblages across habitats. The significant differences in community metrics and their positive correlation to water depth and habitat complexity was consistent with the currently accepted hypotheses of fish-habitat interactions that are largely based on Northern Hemisphere observations (e.g. Cowx & Welcomme 1998; Martin-Smith 1998; Robertson & Winemiller 2003). Our results build on previous findings that these hypotheses appear to hold true for Australian rivers (Pusey *et al.* 1993, 2000; Bishop *et al.* 2001; Kennard *et al.* 2006), and here as elsewhere, fish likely respond to combinations of variables in some hierarchical manner (Rabeni & Jacobsen, 1993; Rayner *et al.* 2008; Bouska & Whitledge 2014). Many Northern Hemisphere studies have indicated that water quality variables, such as temperature, to be influential in species distributions and nestedness at a local scale (see Cook *et al.* 2004; Nykänen *et al.* 2004; Smith & Kraft 2005). Few such relationships were recorded in the LOR, probably reflecting the lack of spatial and temporal variation in water quality variables for the habitats assessed.

A seasonally dynamic fish community structure within habitat patches was also to be expected given the variable flow conditions in the LOR. Greater discharge in the late wet season resulted in greater water velocities than in the dry, particularly in pools (mean velocity of 36 cm s^{-1} *cf* 14 cm s^{-1}). Water depths showed a similar response. It was noticeable that catches from pools were reduced in the wet. Whilst higher velocities in the wet may have reduced the fishing efficiency of gill nets in pools, these reduced catches were counter-balanced by increased catches in the relatively sheltered deep backwater and flooded riparian habitats where velocity was lower. The same change in distribution in the LOR has been subsequently recorded across habitats in the late dry season (November 2005) and late wet season (May 2006) when sampling by gill net and electrofisher boat (A. Storey, unpub. data). During the current study, water levels in previously shallow backwaters had risen 2–3 m by the late wet season, connecting these habitats to the main channel via areas of flooded riparian vegetation. Therefore, these 'backwaters' no longer

provided shallow (0.5 m deep), standing water habitat for small species/juveniles. Instead, the now deep (2.2 m), low flow areas (8 cm s^{-1}) were colonised by larger-bodied species that normally resided in pools in the main channel. Similarly, broad benches covered with riparian vegetation exposed in the dry were transformed by inundation in the wet season (~ 2 m deep), providing habitat with velocities lower than those of main channel pools and areas of emergent vegetation. It would appear that species and life stages actively moved to remain within their preferred range of ambient conditions. Seasonal and ontogenetic differences for a range of fish species have been demonstrated elsewhere (Scheideggar & Bain 1995; Grossman & Ratajczak 1998; King *et al.* 2003; Nykänen *et al.* 2004), with these studies indicating that optimum conditions typically exist only for relatively narrow zones within habitat patches. During the wet season, vertical segregation is also likely to play a greater role in enabling co-existence of multiple species and life stages in the deepwater habitats, however, this aspect was not directly addressed by the current sampling regime.

Sampling limitations

Sampling methods used in the current study were those readily available and considered most effective to maximise abundance and diversity of fishes in the habitats being surveyed; multipanel gill nets in deeper water and seine netting in shallow water. Multipanel gill nets are effective across a range of habitats, except in shallow water habitats. Whereas seine netting is effective in shallow waters, but not in deep water habitats. It is acknowledged that neither method is ideal as seine netting will likely bias towards large numbers of small bodied, and less mobile species, whilst gill netting will likely bias towards mobile, larger-bodied species. Sampling with the seine net, especially in shallow backwaters was considered very effective, as the whole backwater was seined, and sequential seine hauls through backwaters seldom caught additional taxa after the first haul (A. Storey, unpubl. data). Therefore species richness for backwaters is considered accurate, and the absence of larger-bodied species a good reflection of assemblage composition. Subsequent sampling of fish assemblages of selected deepwater habitats in the Ord using gill nets and boat electrofishing (A Storey & A Berguis, Qld DPI Unpub. dat.), showed gill nets captured approximately 85% of the species taken by electrofishing. Occasional specimens of sedentary species were caught by the electrofisher but not by gill netting, such as sleepycod *Oxyeleotris selheimi*. The boat electrofisher also occasionally caught small-bodied species such as *Glossogobius giuris*, *Melanotaenia australis* and *Craterocephalus stramineus*. However, these latter species tended to be taken when the electrofisher boat moved into shallow areas along the bank, rather than from deep water, pool habitat *per se*. Allowing for these differences, gill netting and boat electrofishing provided very similar assemblage data, suggesting gill nets do represent fish assemblages of the habitats sampled in the LOR. Even so, the inherent problems in comparing catch data from different methods over different spatial scales are well documented (Maunder *et al.* 2006) and are a consideration in the current study.

Species-, age- or size-selectivity of techniques and catchability of species means that individual methods are not always comparable, and this undoubtedly holds true for the current study. Unfortunately there is no single sampling technique that is effective across multiple habitats, particularly in large, spatially complex rivers such as the LOR. If habitat use by fishes is to be compared across multiple habitats, then a combination of techniques is justified if each method provides a true representation of fish assemblages in each habitat. It is considered that methods used in this study meet this objective, but even so, observed trends in the data were interpreted with due consideration of capture method. Comparing species richness across methods, particularly where one method catches greater abundances than another, is prone to error (Gotelli & Colwell 2001), because species richness is known to increase with abundance of specimens captured (Chao et al. 2005; Ebner et al. 2008). Therefore, direct comparison of species richness of samples with high abundance against those of lower abundance may be misleading. Rarefaction of samples (Gotelli & Colwell 2001) was used to re-estimate species richness and thereby reduce the effect of sampling method on species richness.

Results from this study align with those reported extensively in the literature. Power (1984), Power et al. (1985) and Schlosser (1987) all reported habitat segregation, whereby large piscivorous fish forced small fish into shallow refuges. Similarly, Finger (1982), Schlosser (1982a, b), Moyle & Baltz (1985) and Bain et al. (1988) all noted that shallow and slow-flowing areas were used by small, young fish of several species, and deep areas were primarily inhabited by larger, older fish. This concordance provides confidence in the efficacy of the methods utilised in this study.

Ecologically relevant water provision

If the biotic integrity of the LOR is to be maintained, then the risk posed by water abstraction should be assessed at the habitat scale, and particularly in the dry season when habitats were most distinct, species preferences the highest, and shallow habitats the most susceptible to change due to reduced water levels (Trayler et al. 2002; Storey & Trayler 2006). The current study demonstrates the importance of shallow-water habitats to small-bodied species and juveniles of larger species. Hydrological studies have indicated that even small changes in depth are likely to substantially alter the availability of shallow water habitats in the LOR (Trayler et al. 2002; Storey & Trayler 2006), and given the clear preference of small fishes for these habitats, a reduction in lateral habitat will potentially lead to a loss of biodiversity. Relationships between shallow habitats and fish assemblages have been reported previously. Cowx & Welcomme (1998) report shallow, lateral habitats as important for young-of-the-year fish, providing low velocity zones, food resources, protection from deep-bodied piscivores and physical cover, with an increase in area of lateral habitat resulting in increased density of age-0 fish, but a reduction in lateral habitat correlated with elimination of young-of-the-year fish (Cowx & Welcomme 1998). And in an impounded river in southeastern Wyoming, Patton & Hubert (1993) considered that continued loss of shallow backwater and side-channel habitats as a result of

reduced flows would lead to loss of species from the system.

Of the 38 species recorded in the current study, autecology has been detailed for at least 20, but is based predominantly on surveys of populations in the Alligator Rivers region, approximately 800 km east of the Ord River system (see Bishop et al. 2001), and Queensland (see Pusey et al. 2004). It is not known if the biology of these species is the same in the heavily regulated LOR as in their natural habitat, or how species have adapted to the modified flow regime. A number of the species detailed by Bishop et al. (2001) and Pusey et al. (2004) use densely vegetated, seasonally inundated floodplain habitats for spawning and larval nursery areas. Though spawning is not necessarily restricted to the floodplain, there is increasing evidence from studies of other Australian river systems that floodplains and flooding play an important role in the general ecology of many freshwater fishes (Koehn 2000; Puckridge et al. 2000; Schiller & Harris 2001; Balcombe et al. 2007). In the LOR however, connectivity with the historic floodplain has been lost as current regulation prevents wet season flows of sufficient magnitude. It seems likely that floodplain-adapted species must now use the flooded margins of the main channel which lies within the historic active channel. However, the lack of locally derived autoecological information of some species and the complete lack of such information for others, needs redress if the LOR is to be managed in an informed manner, and if tropical rivers in Australia in general are to be managed sustainably.

Maintenance of habitat required by all life stages is critical to the survival of a species, and an inadvertent loss of a key habitat(s) could result in a decline in species diversity. The current study only examined a limited suite of habitats on two occasions, and did not consider the broader context of habitat usage. Cowx and Welcomme (1998) noted that fish in rivers depend on undamaged interactive pathways along four dimensions: longitudinal, lateral, vertical and temporal. Such observations have lead researchers to theorise on the "plasticity" of habitat use whereby fish assemblages can behave either as guilds (associated with discrete habitats) or as part of a continuum, with species responding to individual environmental gradients (see Grossman & Ratajczak 1998; Pusey et al. 2000; Erős et al. 2005). In our analyses, not all variation in fish assemblages could be explained by measured abiotic variables. Pusey et al. (2000) obtained similar results from predictive modelling on four rivers in Queensland, Australia. They suggested that this, coupled with high dissimilarity in fish assemblage composition (as is also reported here) reflected the complexity of habitat segregation between species and life history stages. Assessment of the quality and quantity of a specific habitat in an instance in time, although an important means of considering faunal habitat, may be inadequate and misleading if other spatial or temporal habitat requirements are ignored. For example, habitat for adults may be well managed, but if the specific habitat required by larval or juvenile stages is not available (i.e. low velocity, shallow backwaters), then the species may not proliferate. Nor should habitat patch dynamics be viewed as consistent between faunal groups, especially where they operate at different spatial and temporal scales. Functional habitats for fish are

unlikely to correspond precisely to those of macroinvertebrates (*cf* Storey & Lynas 2007). Thus for fishes in the LOR, water depth and velocity are more useful for discriminating functional habitats, whereas percentage cover by cobble substrate and emergent/ submerged vegetation were reported as being important for discriminating habitats for macroinvertebrates (Storey & Lynas 2007).

Buffagni *et al.* (2000) considered that it was possible to maintain specific functional habitats to protect endangered or rare species, or to modify channel morphology to increase hydraulic and habitat heterogeneity. Such applications have commenced in the United Kingdom (Kemp *et al.* 1999), and in northern Italy (Buffagni 2000), where flow was related to occurrences of functional habitat, rather than to taxa preferences for water depth and velocity. Overall, these studies support the use of the FHC in river management. However, without detailed knowledge of life history requirements of resident species it may not be possible to predict all implications of flow regulation. Given the presence of 'functional habitats' in the LOR, the application of the FHC seems an appropriate tool for future management of this river.

This study identified deep channel and shallow, marginal habitats as being important to different components of the fish fauna. Hydraulic modelling has indicated that shallow-water habitats in the dry season are most likely to be affected by further abstraction from this already heavily regulated system (Trayler *et al.* 2002). This potentially places the fauna of these habitats at threat. Although the hydrology of the system is already highly modified, it still supports substantial ecological value, a reflection of establishing a permanent water source in a seasonally dry region. This was acknowledged by the Western Australian Environmental Protection Authority who recommended that any environmental flow should maintain the riverine environmental values established since the construction of the ORD (Trayler *et al.* 2002; Storey & Trayler 2006). Although controversial, this pragmatic decision acknowledged the current, modified, yet arguably high values of the system, and that the dams were not going to be removed (see Storey & Trayler 2006). Our inference is that maintenance of the current array of habitats will help support the current values. Environmental flows for the LOR must be designed to protect and maintain the current distribution and area of these key habitat types to maintain their dependent faunas (*sensu* Buffagni *et al.* 2000). The challenge for hydrologists/ fluviomorphologists is to predict how the distribution of these habitats may change under a new flow regime, a generic issue discussed by Tickner *et al.* (2000). The LOR has a predictable and relatively constant dry season flow however wet season flows are more variable, influenced by infrequent but high magnitude tropical cyclones and monsoon depressions. These events, as has been seen in 2000 and 2001, can re-distribute sediment beds, expose snags, and scour submerged macrophyte beds from the channel. This study provides a snap-shot of habitats and their usage in one wet and one dry season. In reality, multiple years of monitoring of functional fish habitats, across years when certain habitats vary in their availability by orders of magnitudes (i.e. submerged macrophyte beds), ultimately will be required to obtain a better understanding of the influence of water availability on the function and structure of the Lower Ord fish assemblages and habitats.

Given the physically distinct nature of the identified functional habitats, a program to monitor their extent over time was developed in 2003 (A. Marshall & A. Storey, unpub. data). The approach uses high resolution (0.25 m), low level (4 000 ft) digital aerial photography of the channel to quantify the area of each functional habitat as identified for fish (this study) and macroinvertebrate assemblages (Storey & Lynas 2007). In late 2006, the recommended approach was applied to three reaches on the LOR, each 5 km in length. It was recommended that monitoring be conducted in the late dry season over three years prior to and three years after a new flow regime is implemented, to test for any changes in key 'functional' habitats. Subsequent to these investigations, the environmental flow regime for the LOR has been designed to maintain functional habitats, and their associated faunas (WRC 2013).

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APPENDIX

Fish species, number caught and size ranges recorded over two consecutive seasons (late dry and late wet) from eight habitats in the LOR. Codes: FL = fork length, i.e. snout to fork of tail or snout to posterior margin of tail for eel-tailed species; LFM = length at first maturity as estimated by Bishop et al. (2001) for fishes in the Alligator River catchment of the Northern Territory. Where LFM differed by > 3mm between sexes, size is indicated for both females (F) and males (M).

Family	Species	Common name	FL mm	LFM mm	Numbers caught Late dry	Late wet
Ambassidae	Ambassis macleayi (Castelnau,1878)	Macleay's glassfish	14–53	~30	38	606
	Ambassis sp. (undescribed)	Northwest glassfish	27–65		460	3
	Parambassis gulliveri (Castelnau, 1878)	giant glassfish	29–54		33	21
Anguillidae	Anguilla bicolor bicolor McClelland, 1844	Indian short-finned eel	310		1	184
Apogonidae	Glossamia aprion (Richardson, 1842)	mouth almighty	19–119	~65	7	4
Ariidae	Neoarius graeffei (Kner & Steindachner, 1867)	lesser salmon catfish	85–484	~300	197	1
	Neoarius midgleyi (Kailola & Pierce, 1988)	silver cobbler	160–633		57	32
	Sciades leptaspis (Bleeker, 1862)	triangular shield catfish	230–538	~300	11	0
Atherinidae	Craterocephalus ?stercusmuscarum (Günther, 1867)	Fly-specked hardyhead	23–38	~28	23	26
Belonidae	Strongylura krefftii (Günther, 1866)	freshwater longtom	189–413	290M, 410F	11	4
Carcharhinidae	Carcharhinus leucas (Müller & Henle, 1839)	bull shark	554–1200	>2000	6	12
Latidae	Lates calcarifer (Bloch, 1790)	barramundi	130–731	700M, 900F	37	42
Clupeidae	Nematalosa erebi (Günther, 1868)	bony bream	20–363	130M, 140F	72	318
Dasyatidae	Himantura dalyensis Last & Manjaji-Matsumoto 2008	freshwater whipray	600–1250		1	2
Eleotridae	Hypseleotris compressa (Krefft, 1864)	empire gudgeon	22–66	37M, 43F	42	3
Elopidae	Elops hawaiensis Regan, 1909	giant herring	337–473		1	1
Engraulidae	Thryssa sp.		125–128		4	1
Gobiidae	Glossogobius giuris (Hamilton, 1822)	flathead goby	47–92	~35	39	15
	Gobiidae sp. B		25		1	0
Hemiramphidae	Arrhamphus sclerolepis sclerolepis Günther, 1866	garfish	203		1	0
Leiognathidae	Leiognathus equulus (Forsskål, 1755)	ponyfish	37–73		90	4
Megalopidae	Megalops cyprinoides (Broussonet, 1782)	ox-eye herring	120–412	>300	12	11
Melanotaeniidae	Melanotaenia australis (Castelnau, 1875)	western rainbowfish	21–70	23	137	106
Mugilidae	Liza alata (Steindachner, 1892)	diamond mullet	31–470	>350	478	189
	Mugillidae sp.		95		0	1
Plotosidae	Neosilurus hyrtlii Steindachner, 1867	Hyrtl's tandan	155–455	135	8	11
	Plotosidae sp. 1		50–97		0	4
	Plotosidae sp. 2		56–69		0	1
Pristidae	Pristis pristis (Linnaeus, 1758)	freshwater sawfish	765		0	1
Scatophagidae	Scatophagus argus (Linnaeus, 1766)	spotted scat	23–122		0	2
Sciaenidae	Nibea squamosa Sasaki, 1992	scaly croaker	384		0	1
Soleidae	Leptachirus triramus Randall, 2007	tailed sole	51–59		0	3
Terapontidae	Amniataba percoides (Günther, 1864)	barred grunter	19–89	45F, 65M	54	165
	Hephaestus jenkinsi (Whitley, 1945)	Jenkin's grunter	166–345		0	2
	Leiopotherapon unicolor (Günther, 1859)	spangled perch	96–129	74M, 94F	4	3
	Syncomistes butleri Vari, 1978	Butler's grunter	100–273	235	3	17
Tetraodontidae	Marilyna meraukensis (de Beaufort, 1955)	Merauke toadfish	61–136		16	4
Toxotidae	Toxotes chatareus (Hamilton, 1822)	seven-spot archerfish	24–272	180M, 190F	33	86